

Neural integration in body perception

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Title: Neural integration in body perception

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Abstract

The perception of other people is instrumental in guiding social interactions. For example, the appearance of the human body cues a wide range of inferences regarding sex, age, health and personality, as well as emotional state and intentions, which influence social behaviour. To date, most neuroscience research on body perception has aimed to characterise the functional contribution of segregated patches of cortex in the ventral visual stream. In light of the growing prominence of network architectures in neuroscience, the current paper reviews neuroimaging studies that measure functional integration between different brain regions during body perception. The review demonstrates that body perception is not restricted to processing in the ventral visual stream, but instead reflects a functional alliance between the ventral visual stream and extended neural systems associated with action perception, executive functions and theory-of-mind. Overall, these findings demonstrate how body percepts are constructed through interactions in distributed brain networks and underscores that functional segregation and integration should be considered together when formulating neurocognitive theories of body perception. Insight from such an updated model of body perception generalises to inform the organisational structure of social perception and cognition more generally, and also informs disorders of body image, such as anorexia nervosa, which may rely on atypical integration of body-related information.

Key words: Body perception; fMRI; functional connectivity.

1. Introduction

The appearance of the human body provides a rich source of social information. Bodies signal cues to an observed individual's sex, age, health and personality, as well as his or her emotional states and intentions. Such signals are important for social interactions, as they guide human behaviour in terms of approach/avoidance tendencies, mate selection and cooperation. Given their instrumental influence on daily life, research has aimed to identify the neurobiological mechanisms by which such signals are detected, processed and utilised (Frith & Frith, 2010).

Research investigating the perception of other people – social perception – has been dominated by the study of faces (Bruce & Young, 1986; Duchaine & Yovel, 2015; Haxby et al., 2000; Kanwisher, 2010; Jack & Schyns, 2017). Faces play a central role in social interactions and, as a consequence, face perception research has provided valuable insights. However, bodies also cue a range of information that is exploited during social interactions (de Gelder et al., 2010), which, at times, faces conceal (Aviezer et al., 2012). Therefore, if a core aim of social perception research is to understand how we read and navigate social signals in the real world, bodies are also a vitally important cue to study. Moreover, bodies, like faces, can be studied as a model system to investigate the cognitive and neural processes that underpin social perception.

The majority of neuroscience research on body perception has focussed on understanding the role of segregated patches of cortex in the ventral visual stream (for reviews, see Downing & Peelen, 2011; 2016). This work has identified two regions of ventral temporal cortex (fusiform body area: FBA; Extrastriate body area, EBA) that respond more robustly to bodies than other classes of stimuli, such as houses and chairs. FBA and EBA, therefore, are said to show category-selectivity for bodies. Although many functional claims

have been made for the role of these two regions, the majority of evidence suggests that these regions primarily process body shape and posture (Downing & Peelen, 2011).

Complicated mental processes, such as those underpinning aspects of social perception, are unlikely to rely solely on segregated patches of cortex acting alone, however (Kanwisher, 2010; Ramsey et al., 2011). Rather, mental processes are likely to involve the integration of interacting signals that span across distributed neural networks (Bullmore & Sporns, 2009; Fuster, 1997; Mesulam, 1990). Indeed, two cornerstones of brain function are functional segregation and functional integration (Park & Friston, 2013). Functional segregation is characterised by information processing that is carried out by functionally related brain regions that are arranged in modules¹, whereas functional integration involves the exchange of signals across a distributed set of such brain networks or modules (Park & Friston, 2013; Sporns, 2013). Given the range and complexity of social information that bodies are associated with, responses in ventral temporal cortex are likely to be a combined product of local, as well as distributed, processing functions (Sporns, 2013). To date, however, little is known about the role of functional integration in body perception.

The main aim of the current paper is to review neuroimaging evidence for functional integration in body perception and consider the implications of functional integration research for understanding the neural bases of social perception. The paper is organised in four parts. First, to provide a relevant context, a brief review of evidence for functional segregation in body perception is provided. Second, evidence from functional magnetic resonance imaging (fMRI) studies that have investigated functional integration in body perception are reviewed. These studies show that brain circuits in ventral temporal cortex and those in extended networks associated with action perception, executive functions and

¹ The term ‘module’ refers only to functionally related brain regions. It does not refer to additional features that were initially proposed by Jerry Fodor to define information processing modules (Fodor, 1983).

theory-of-mind integrate information during body perception. Together, the first two sections of the paper suggest that by considering functional segregation and integration together, we will have a more complete understanding of the neural systems that support body perception. Third, the implications of such an updated neurocognitive model of body perception for understanding social perception and cognition more generally, as well as disorders of body image, are discussed. Finally, future directions that embrace network science approaches to understanding social perception are outlined.

2. Functional segregation in body perception

A primary neuroimaging method for identifying category-selectivity in the human brain has been to adopt a functional region of interest approach (fROI; Kanwisher, 2010; 2017). The fROI approach typically uses univariate methods for comparing responses across different categories of stimuli. First, regions of interest are identified based on functional data using a “localiser” scan, before the response in these regions is interrogated using separate task data. This approach has identified two body-selective regions in ventral temporal cortex (FBA and EBA), which respond to bodies more than other object categories such as houses and chairs (Figure 1A; Downing et al., 2001; Peelen & Downing, 2005; Zhan et al., 2018; for a review, see Downing & Peelen, 2011). Functional divisions have also been identified within this body circuit with FBA showing greater sensitivity to whole bodies and EBA showing greater sensitivity to body-parts (Taylor et al., 2007).

While there is clear evidence for body shape and posture processing in FBA and EBA, more elaborate cognitive processes have also been ascribed to these regions including identity, emotion, and action-related processes (Downing & Peelen, 2011). However, there is less convincing evidence for these more elaborate representations in ventral temporal regions (Downing & Peelen, 2011). Like the majority of brain networks, responses in ventral

temporal cortex are likely to index a local processing function as well as an exchange of signals within a wider neural network (Sporns, 2013). As such, claims based on univariate responses in EBA and FBA may reflect the exchange of signals with wider brain networks in addition to local processes (Park & Friston, 2013). This is especially the case for more elaborate representations associated with social cognition, which have been shown to recruit a widely distributed neural architecture (Frith & Frith, 2010; Figure 1B). Evidence for interactions between body-selective areas in ventral temporal cortex and wider networks associated with social perception and cognition are reviewed in the next section.

3. Functional integration in body perception

Complex mental processes, such as those subserving social perception and social inference, are unlikely to rely on a narrow use of neural tissue that is restricted to ventral temporal cortex (de Gelder, 2006; Duchaine & Yovel, 2015; Haxby et al., 2000; Kanwisher, 2010; Ramsey et al., 2011). Models of emotional body perception, for example, are based on a distributed and interacting set of brain networks (de Gelder, 2006; de Gelder et al., 2015). To measure network connectivity, neuroimaging methods have been developed that enable interactions between distinct anatomical or functional regions to be estimated (Friston, 2011). Although many connectivity studies measure resting state activity (Greicius et al., 2003), other studies measure how connectivity changes as a function of the experimental condition, such as the type of task or stimulus (Friston, 2011; Friston et al., 1997).

Such task-based functional connectivity approaches substantially extend univariate approaches by first identifying functional regions of interest using established localisers, and then estimating how these networks interact as a function of the task or stimulus set. At least two broad classes of task-based connectivity have been developed: directional and correlational. Directional measures of functional connectivity, such as Dynamic causal

modelling (DCM) and Granger causality, permit inferences to be drawn regarding the direction of influence of one brain region on another (Friston, 2009). In contrast, purely correlational measures, such as PsychoPhysiological Interactions (PPI), are unable to provide an estimate of the direction of influence (Friston et al., 1997; McLaren et al., 2012). Instead, PPI relies on general linear modelling to estimate how correlations between brain regions vary as a function of task demands. Importantly, PPI modelling procedures typically include univariate and PPI regressors within the same model, which means for PPI regressors to be of interest, they must explain variance above and beyond that explained by the univariate regressors (McLaren et al., 2012; O'Reilly et al., 2012).

Although it has been proposed that body perception involves a distributed neural architecture that extends beyond ventral temporal cortex (e.g., de Gelder, 2006; Ramsey et al., 2011), fewer than ten studies have investigated functional integration during body perception using fMRI. Univariate neuroimaging techniques, as well as neuropsychology lesion studies, show that recognising emotional body postures relies on a distributed neural architecture that extends beyond ventral temporal cortex (for reviews, see de Gelder, 2006; de Gelder et al., 2015). However, the lack of functional connectivity studies means that the boundary conditions that govern local processing and distributed processing in body perception remain unclear (Figure 1C). Indeed, neural integration research in body perception has only just begun to identify which neural circuits interact with ventral temporal cortex and in which social contexts. In this section, I focus on studies that have used fMRI and measures of task-based connectivity during body perception. These studies have investigated the relationship between body perception and a range of different topics including identity recognition, action perception, executive control and theory-of-mind.

3.1 Integration within the ventral visual stream

Ewbank and colleagues (2011) used a repetition suppression design to investigate functional interplay between FBA and EBA during the processing of physical identity. Repetition suppression is observed when a repeat stimulus feature produces a reduced neural response and has been used to test population coding models of perception and cognition (Grill-Spector et al., 2006; Barron et al., 2016). In Ewbank and colleagues' (2011) study, participants observed body images that varied in size, orientation and identity. When there was a repeat identity, both FBA and EBA showed a reduced response, thus showing repetition suppression for person identity. In addition, Ewbank and colleagues (2011) used DCM to show that FBA modulated responses in EBA for a repeated compared to a novel identity. This response was invariant to changing size and view of the body. The authors suggest that FBA provides top-down control over the response in EBA. Such an interpretation is consistent with the view that FBA represents whole bodies (irrespective of size and viewpoint changes), and influences a more granular, body-part specific representation in EBA that is tuned by body size and view (Taylor et al., 2007). Hence, this study shows that body identity processing is not only a product of local responses in FBA and EBA, but instead reflects integration between these two nodes (Figure 2A).

3.2 Integration between the ventral visual stream and the action perception network

In addition to integration between EBA and FBA, other studies have shown that body patches interact with wider neural networks associated with action perception, executive functions and theory-of-mind. In terms of action perception, Zimmerman and colleagues (2013) showed that body posture modulates the perception of another's action goals. The authors found that when a participant's body posture matches an observed action, the prediction of another's action goal is facilitated. In support of this goal ascription process, the intraparietal sulcus was engaged more when there was a mismatch between the participant's

body posture and the observed action goal posture. In addition, using PPI, the response in intraparietal sulcus correlated with EBA as a function of action frequency: observing low frequency actions increased coupling. The authors interpret the neuroimaging results within a predictive framework, under the assumption that body perception signals in ventral temporal cortex contribute to a prediction of a person's likely goal. The goals associated with more frequently observed actions are less surprising and result in lower prediction error. By contrast, less frequent actions produce a higher prediction error and thus a greater signal exchange between intraparietal sulcus and EBA is required to update the goal estimate (Figure 2B). These results, therefore, document a link between ventral temporal cortex and brain regions associated with the perception of action goals.

3.3 Integration between the ventral visual stream and executive functions

Perception in general, whether of objects, scenes or people, has been shown to involve interplay between the visual stream and neural systems associated with executive functions (Baldauf & Desimone, 2014; Bar, 2004). Executive functions are a set of mental processes that are needed to accomplish difficult tasks, when relying on automated processes would be ineffective (Diamond, 2013). Using a paradigm that manipulated the presence of sex-based stereotypes, processes associated with body perception have been shown to have a similar interactive relationship with executive functions (Quadflieg et al., 2011). When we meet other people, we categorise them into social groups based on many factors, such as sex, age, profession and race. We also hold stereotyped expectations for such social groups, which influence social interactions (Brewer, 1988; Fiske & Neuberg, 1990; Macrae & Quadflieg, 2010). For instance, we typically expect nurses to be female and courtroom judges to be male. In some instances, however, individuals violate stereotypical expectations (e.g., a male nurse). When performing sex judgments of others in situations that violate sex-based

stereotypes compared to those that conform, Quadflieg and colleagues (2011) showed increased coupling between dorsolateral prefrontal cortex (dlPFC) and body-selective patches in the ventral visual stream. The authors suggest that dlPFC modulates visual processing of object categories, in this case bodies, in order to override the initial expectation based on bodies and to modulate the formation person percepts in the brain (Figure 2C).

3.4 Integration between the ventral visual stream and the theory-of-mind network

Theory-of-mind is the attribution of mental states, such as beliefs, desires and attitudes, to others and has been consistently associated with the engagement of medial prefrontal cortex, temporoparietal junction, temporal poles and precuneus (Frith & Frith, 1999; Saxe & Kanwisher, 2003; van Overwalle, 2009). The theory-of-mind network responds to a variety of tasks involving mental attribution and social inferences (van Overwalle, 2009) and can be reliably identified with a short belief reasoning functional localiser during fMRI (Dodell-Feder et al., 2011).

Using body perception and theory-of-mind localisers, a series of studies has investigated the relationship between body-selective patches in ventral temporal cortex and the theory-of-mind network during body perception (Figure 2D; Greven et al., 2016; 2018; Greven & Ramsey, 2017a, b). Each study investigated a distinct component of social information processing during body perception, including the formation (Greven et al., 2016) and recall (Greven & Ramsey, 2017a) of impressions, the impact of group bias on body perception (Greven & Ramsey, 2017b), as well as person inferences that are based on body shape alone (Greven et al., 2018). The broad hypothesis across these experiments was the same: social information processing during body perception will not be restricted to univariate responses in segregated networks, but will also be indexed by integration between body-selective and theory-of-mind networks.

The first study investigated the formation of impressions during body perception (Greven et al., 2016). In a 2 x 2 factorial design, bodies or names were shown to participants alongside a short statement that described behaviours that cued trait-based or neutral judgements (Figure 2D). For example, the statement “She gave money to charity” cues a trait-based inference (e.g., selfless, generous), much more than a trait-neutral statement such as “She sharpened her pencil”. Therefore, the type of inference (trait-based, neutral) and the social target (body, name) were manipulated, and participants were asked to form an impression of the person. Prior work had demonstrated that compared to neutral statements, trait-based inferences engage the theory-of-mind network (Ma et al., 2011; Mitchell et al., 2006). Using PPI, Greven and colleagues (2016) showed that FBA showed stronger functional coupling with TPJ and temporal poles when participants formed an impression of a body, compared to when they formed similar impressions based on a person’s name. This suggests that when forming impressions of others, functional connectivity between FBA and nodes in the theory-of-mind network are tuned to specific types of social information (bodies more than names; trait inferences more than neutral judgments).

Although first impressions are common, much of our daily lives involve interactions with familiar people (e.g., friends, family and colleagues). As such, we have a rich set of stored person associations, which we rely upon to guide social exchanges. To assess recall of social knowledge that is prompted by body perception, in a subsequent study Greven & Ramsey (2017a) trained participants before scanning to associate different bodies with trait-based or neutral information. During scanning participants viewed the same bodies and were asked to form an impression of the individual. PPI analyses showed that perceiving bodies that prompted the recall of social knowledge compared to bodies associated with neutral knowledge engaged more functional coupling between EBA and the temporal poles. These results may suggest that the detection of body parts in EBA triggers an exchange of signals

with a node in the theory-of-mind network that has consistently been associated with the development of person knowledge (Olson et al., 2013). One possible interpretation of this result is that once identity is established based on body shape and posture cues, there is a relatively rapid exchange with a non-visual person knowledge representation in the temporal poles.

In addition to stored knowledge regarding trait-based character, we readily recognise others as being part of an ingroup or outgroup based on factors such as sex, profession, race, and age. Such group biases are prevalent in social perception and cognition and we typically perceive in-group members more favourably than out-group members (Allport, 1954; Brewer, 1999). We are also more likely to remember positive information about ingroup members and more negative information about outgroup members (Fyock & Stangor, 1994). In terms of neural circuits, a distributed set of brain networks are sensitive to group biases, which span visual, affective and cognitive systems (Amodio, 2014; Molenberghs, 2013). However, little is known regarding functional connectivity between these neural circuits during group bias modulation of person perception. Greven & Ramsey (2017b) used a minimal-group manipulation (Tajfel et al., 1971), whereby participants were randomly assigned to a “blue” or “yellow” team and given a long-sleeved t-shirt to wear, which matched their team colour. Participants were subsequently shown images of ingroup and outgroup members (i.e., those wearing blue or yellow t-shirts), who were previously associated with positive or negative social information. PPI results showed greater coupling between FBA and TPJ for bias-consistent (ingroup-positive and outgroup-negative) than inconsistent pairings. These results suggest that coupling between the ventral visual stream and the theory-of-mind network is tuned to social knowledge and social group pairings. Indeed, interactions between networks is not driven by main effects of group or valence, but

instead reflects the combination of the two types of information (ingroup, good; outgroup, bad).

Impressions are not only formed based on explicit knowledge of behaviour; impressions are also formed based on physical shape alone. For example, body shape and posture cue inferences regarding emotional state, personality and health (Borkenau & Liebler, 1992; de Gelder et al., 2010; Puhl & Heuer, 2009; Sell et al., 2009). Using silhouette images of bodies, which emphasise body shape and posture cues, Greven and colleagues (under review) performed two fMRI experiments that investigated the neural bases of inferences that are drawn from body shape alone. Before scanning, three behavioural experiments showed that different body types (obese, muscular) were judged differently on dimensions of personality and health compared to slim bodies. Obese bodies were rated as less extraverted, conscientious, and healthy, whereas muscular bodies were rated as more extraverted and healthy, but less agreeable. These results show that social inferences of slim bodies are more neutral (i.e., closer to the middle of the rating scale) when evaluating personality and health than muscular and obese bodies. This does not imply an absence of social inferences for slim individuals, just that inferences are less extreme. In other words, social inferences are made for all body types and only the content of these inferences varies based on the physical attributes of the bodies. As part of the same study, two subsequent fMRI experiments used the same stimuli, but varied the task. The first experiment used a one-back recognition task and showed no evidence for differential engagement of body or theory-of-mind networks and no coupling between body and theory-of-mind networks. In the second experiment, which required participants to form an impression of the person, evidence emerged for functional coupling between EBA and the temporal poles, but it was a relatively weak effect. There was, however, clearer evidence for differential engagement of segregated neural circuits: the Muscular > Slim contrast engaged EBA and FBA, whereas the Obese > Slim contrast

engaged mPFC and temporal poles. These results suggest that there is a division of labour between body and theory-of-mind networks when forming an impression based on body shape.

Together, this series of four fMRI studies shows that different dimensions of body perception involve functional interplay between body and theory-of-mind networks. These dimensions include: 1) Stage of social knowledge acquisition (formation vs. recall); 2) The form of social knowledge (written description vs. body shape); 3) Identity of the social target (ingroup vs. outgroup), and; 4) Intentionality of social inference (unintentional vs. intentional). Considering the results of these studies together suggests that the ventral visual stream and the theory-of-mind network do not act in isolation during body perception, but instead exchange signals across multiple social information processing dimensions.

Further, the results permit speculation on a possible division of labour in functional network organisation. Forming impressions of another person's character and tagging such information to body shape is associated with links between FBA and the theory-of-mind network, including the temporal poles and TPJ (Greven et al., 2016). It is possible that developing a richer representation of a person to include non-visual information (i.e., impressions of trait-based character) involves exchange between FBA and temporal poles, which is consistent with the role of TP in stored person knowledge (Olsen et al., 2013) and FBA in a representation of whole bodies (Taylor et al., 2007). It is also consistent with recent work in the domain of face perception, whereby links between the ventral visual stream and temporal poles have been demonstrated to underpin the retrieval of social knowledge that is associated with faces (Wang et al., 2017). By contrast, recall of social knowledge that is prompted by body shape involves links between EBA and temporal poles (Greven & Ramsey, 2017a; Greven et al., 2018). One interpretation is that when bodies cue social inferences, the detection of body parts in EBA (Taylor et al., 2007) triggers an associated

representation of stored social knowledge in temporal poles (Olsen et al., 2013). This proposal is consistent with theories of impression formation that posit links between representations of facial features and trait knowledge (Over & Cook, 2018). However, the possibility that networks can be fractionated into functionally distinct partitions remains speculative at the moment. Indeed, models of neural integration between the ventral visual stream and the theory-of-mind network are only just beginning to be formulated, and it will be important for future work to directly test these predictions using a range of methods (see future directions section).

3.5 Summary

In summary, evidence is emerging that different dimensions of body perception involve functional interplay within the ventral visual stream, as well as between the ventral visual stream and neural networks associated with action perception, executive functions and theory-of-mind (Figure 2). These results demonstrate that the ventral visual stream does not act alone in body perception, but instead forms functional connections with distributed neural networks that span anterior temporal, frontal and parietal cortices. Next, implications for neurocognitive models of body perception are outlined.

4. Implications

The primary implication of the reviewed evidence is that body percepts are constructed through relationships between distributed and interacting neural networks. Indeed, links between the visual stream and extended systems are suggestive that information processing in the visual stream is not sufficient to perceive the outside environment (Gilbert & Sigman, 2007; Sterzer et al., 2009). A consequence of this suggestion for neuroimaging research in general is that focussing on segregation alone will produce skewed models of mental

processes that are biased towards a segregationist structure and underestimate complexity. This is not to suggest that understanding functional segregation holds no value in social perception. Rather, these results underscore that to understand complex mental processes, functional segregation and integration need to be considered in partnership (Sporns, 2013). Indeed, fMRI studies that only use univariate approaches must keep in mind that responses may not only reflect a local, segregated function, but also an integrative function.

Studying the perception of bodies, like faces, scenes, words, and tools, is one way to understand organising principles of human brain function. Here we extend this understanding to show how functionally segregated modules connect to form functionally interacting networks during body perception. Therefore, the reviewed research uses body perception as a model system to investigate mechanisms of social perception, as well as a means to study network models of human brain function more generally. Consequently, the results hold the potential to inform other research domains that also rely on distributed but interacting modules, such as face perception (e.g., Duchaine & Yovel, 2015), object perception (Bar, 2004), and memory (Cabeza & Moscovitch, 2013). For example, similarities are likely to exist between face and body perception (de Gelder et al., 2010), which means core principles from the findings reported here may readily apply to face perception. Relatedly, theories of impression formation, which specify links between the acquisition of trait knowledge and the representation of facial features (Over & Cook, 2018), could be informed by the work reviewed here on links between systems associated with body shape perception and theory-of-mind. As a further example, functional structures in the domains of memory (Cabeza & Moscovitch, 2013) and object perception (Bar, 2004), involve links between domain-specific and domain-general systems, a picture that also emerges in the body perception research reviewed here. As such, by comparing different information processing domains, common

and distinct organising principles of brain function can emerge, which may lead to new hypotheses.

With regard to body perception research more specifically, it is becoming clearer that category-selectivity in ventral temporal cortex cannot be completely reduced to task-invariant processing of visual features (Harel et al., 2014; Bi et al. 2016; Peelen and Downing, 2017). Instead, category-selective responses reflect knowledge of what the object means to the observer, as well as how they interact with it (Peelen and Downing 2017). As such, a wider neural architecture is likely to be important to consider. The reviewed studies begin to probe the boundary conditions that control the relationship between functional segregation and integration and identify which neural circuits interact with ventral temporal cortex and in which social contexts. But integration research is only beginning to scratch the surface of understanding this complex topic and much more research is needed.

A deeper appreciation of network science approaches to body perception may have clinical relevance for body-related disorders. For example, in anorexia nervosa, reduced connectivity between FBA and EBA has been associated with body image distortion (Suchan et al., 2013). More generally, therefore, when considering distortions in body image, it may prove useful to consider the role of wider networks. Problems in body-related information processing may arise from altered integration of body representations as much as altered responses in the ventral visual stream alone.

5. Limitations and future directions

The current review had a purposely narrow focus and did not set out to provide a comprehensive review of body perception research from a cognitive neuroscience perspective. Instead, the review targeted human fMRI research that investigated body perception using measures of functional connectivity. As such, a comprehensive review of

body perception research was beyond the scope of this review. Moreover, detailed reviews have already considered the proposed functions of EBA and FBA (Downing & Peelen, 2011), as well as the contribution from neurostimulation and patient studies to understanding body perception (Downing & Peelen, 2016), and the role of emotion in body perception (de Gelder, 2006; de Gelder et al., 2010). In addition, other work has used direct intra-cranial recordings in humans (Pourtois et al., 2007) and evidence from non-human primates (Bell et al., 2009; Pinsk et al., 2005; 2009) to further understand the neural bases of body perception.

A further consideration also relates to the intended scope of the current review. The current paper was centred on understanding functional connectivity within the ventral visual stream, as well as between the ventral visual stream and broader neural networks. This focus was motivated by the dominance of the ventral visual stream in person perception research to date (Kanwisher, 2010). However, recent body perception research has also shown that coupling between extended networks makes a contribution to emotional body perception (Engelen et al., 2018; Poyo Solanas et al., 2018). For example, using fMRI, Poyo Solanas and colleagues (2018) showed that when faces and bodies convey congruent compared to incongruent emotional signals, there is greater functional coupling between the amygdala and the anterior cingulate cortex. This suggests that the amygdala may provide a regulatory role in responding to unambiguous emotional signals, which are conveyed by face and body concurrently. The results also suggest that coupling in body perception need not be restricted functional interactions that involve the ventral visual stream and future research should pursue this line of research further.

Further future directions stem from three principle limitations of the current evidence. First, a lack of emphasis on functional integration in body perception research hampers understanding of social perception more broadly. Except for models of emotional body perception, which include distributed networks (de Gelder, 2006), there is little research on

body perception more generally that considers functional integration and network approaches. Building on the work reviewed here, further research is required that investigates the boundary conditions that demarcate the reliance on segregated processing in local modules and information processing that is distributed more widely across larger neural networks.

Second, evidence for functional integration in body perception is largely based on correlational datasets. Further methodological development will circumvent a reliance on correlational measures of functional connectivity and increase the prevalence of measures that permit inferences regarding directional (e.g., DCM, granger causality), structural (e.g., Diffusion tensor imaging), and causal relationships (e.g., using neurostimulation techniques combined with fMRI). Finally, functional connectivity studies should embrace best practice from open science (Munafo et al., 2017). For example, an increase in sample sizes will increase statistical power and may also permit analyses based on individual differences across the sample (Dubois & Adolphs, 2016). Moreover, using approaches from neuropsychology, as well as body disorders, has shown promise in understanding mechanisms of body perception and should be used wherever possible.

Third, theories and models of body perception, which include functional integration, currently lack detail and precision. Updated theories of body perception should consider integration as much as segregation, as well as the extent to which particular processes are positioned along a segregation-integration continuum. By doing so, this would build a model of social perception, which stipulates a relative mix between segregation and integration. To aid the articulation of such theories, researchers may consider using Theory Mapping as a tool to develop, illustrate and compare theories (Gray, 2017; www.theorymaps.org). Theory Mapping provides a common language to visualise theories and store them online, thus promoting easier information exchange. The development of theories and models will enable

more precise predictions to be made, thus providing a stronger test of the underlying hypothesis (Meehl, 1990). Harnessing the extensive development of network science approaches, which include graph theory, will also be vital for more sophisticated techniques for specifying and testing models of functional integration with brain data (Bullmore & Sporns, 2009).

Conclusion

Although bodies cue a range of inferences, which are instrumental for guiding social behaviour, we currently know little about the neural organisation of body perception. The current review of evidence from fMRI studies demonstrates that body perception is not restricted to processing in the ventral visual stream, but instead reflects a functional alliance between the ventral visual stream and extended neural systems associated with action perception, executive functions and theory-of-mind. Overall, these findings demonstrate how body percepts are constructed through interactions in distributed brain networks and underscores that functional segregation and integration should be considered together when formulating neurocognitive theories of body perception. By emphasising the importance of network science approaches, the findings have implications for understanding network models of perception and cognition more generally, as well as understanding the biological bases of body image disturbances, such as anorexia nervosa, which are likely to have a complex biological basis.

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References

- Allport, G. (1954). *The Nature of Prejudice*. Cambridge, Massachusetts: Addison-Wesley Publication company.
- Amodio, D. M. (2014). The neuroscience of prejudice and stereotyping. *Nat Rev Neurosci*, advance online publication. doi: 10.1038/nrn3800
- Aviezer, H., Trope, Y., & Todorov, A. (2012). Body Cues, Not Facial Expressions, Discriminate Between Intense Positive and Negative Emotions. *Science*, 338(6111), 1225-1229. doi: 10.1126/science.1224313
- Baldauf, D., & Desimone, R. (2014). Neural Mechanisms of Object-Based Attention. *Science*, 344(6182), 424-427. doi: 10.1126/science.1247003
- Bar, M. (2004). Visual objects in context. *Nat Rev Neurosci*, 5(8), 617-629.
- Barron, H. C., Garvert, M. M., & Behrens, T. E. (2016). Repetition suppression: a means to index neural representations using BOLD? *Philos Trans R Soc Lond B Biol Sci*, 371(1705). doi: 10.1098/rstb.2015.0355
- Bell, A. H., Hadj-Bouziane, F., Frihauf, J. B., Tootell, R. B., & Ungerleider, L. G. (2009). Object representations in the temporal cortex of monkeys and humans as revealed by functional magnetic resonance imaging. *Journal of neurophysiology*, 101(2), 688-700.
- Bi, Y., Wang, X., & Caramazza, A. (2016). Object domain and modality in the ventral visual pathway. *Trends in Cognitive Sciences*, 20(4), 282-290.
- Borkenau, P., & Liebler, A. (1992). Trait inferences: Sources of validity at zero acquaintance. *Journal of Personality and Social Psychology*, 62(4), 645-657. doi: 10.1037/0022-3514.62.4.645
- Brewer, M. (1988). A dual-process model of impression formation In R. S. Wyer Jr. & T. K. Srull (Eds.), *Advances in Social Cognition* (pp. 1-36). Hillsdale, NJ: Erlbaum.
- Brewer, M. B. (1999). The psychology of prejudice: Ingroup love or outgroup hate? *Journal of Social Issues*, 55(3), 429-444. doi: Doi 10.1111/0022-4537.00126
- Bruce, V., & Young, A. (1986). Understanding face recognition. *Br J Psychol*, 77 (Pt 3), 305-327.
- Cabeza, R., & Moscovitch, M. (2013). Memory Systems, Processing Modes, and Components: Functional Neuroimaging Evidence. *Perspectives on Psychological Science*, 8(1), 49-55. doi: 10.1177/1745691612469033
- de Gelder, B. (2006). Towards the neurobiology of emotional body language. *Nat Rev Neurosci*, 7(3), 242-249.
- de Gelder, B., de Borst, A., & Watson, R. (2015). The perception of emotion in body expressions. *Wiley Interdisciplinary Reviews: Cognitive Science*, 6(2), 149-158.
- Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, 64, 135-168.
- Dodell-Feder, D., Koster-Hale, J., Bedny, M., & Saxe, R. (2011). fMRI item analysis in a theory of mind task. *NeuroImage*, 55(2), 705-712. doi: 10.1016/j.neuroimage.2010.12.040
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470-2473.
- Downing, P. E., & Peelen, M. V. (2011). The role of occipitotemporal body-selective regions in person perception. *Cognitive Neuroscience*, 1-24. doi: 10.1080/17588928.2011.582945
- Downing, P. E., & Peelen, M. V. (2016). Body selectivity in occipitotemporal cortex: Causal evidence. *Neuropsychologia*, 83, 138-148. doi: 10.1016/j.neuropsychologia.2015.05.033
- Dubois, J., & Adolphs, R. (2016). Building a Science of Individual Differences from fMRI. *Trends in Cognitive Sciences*, 20(6), 425-443. doi: 10.1016/j.tics.2016.03.014

- Duchaine, B., & Yovel, G. (2015). A Revised Neural Framework for Face Processing. *Annu Rev Vis Sci*, 1, 393-416. doi: 10.1146/annurev-vision-082114-035518
- Engelen, T., Zhan, M., Sack, A.T., & de Gelder, B. (2018). Dynamic interactions between emotion perception and motor preparation networks for responding to social threat: a combined cTBS-fMRI study. *eNeuro*
- Ewbank, M. P., Lawson, R. P., Henson, R. N., Rowe, J. B., Passamonti, L., & Calder, A. J. (2011). Changes in "Top-Down" Connectivity Underlie Repetition Suppression in the Ventral Visual Pathway. *The Journal of Neuroscience*, 31(15), 5635-5642. doi: 10.1523/jneurosci.5013-10.2011
- Fiske, S. T., & Neuberg, S. L. (1990). A continuum of impression formation, from category-based to individuating processes: Influences of information and motivation on attention and interpretation. *Advances in experimental social psychology*, 23, 1-74.
- Fodor, J. A. (1983). *The Modularity of Mind*. Cambridge, MA: The MIT Press.
- Friston, K. (2009). Causal Modelling and Brain Connectivity in Functional Magnetic Resonance Imaging. *PLoS Biol*, 7(2), e1000033.
- Friston, K. J. (2011). Functional and effective connectivity: a review. *Brain Connect*, 1(1), 13-36. doi: 10.1089/brain.2011.0008
- Friston, K. J., Buechel, C., Fink, G. R., Morris, J., Rolls, E., & Dolan, R. J. (1997). Psychophysiological and Modulatory Interactions in Neuroimaging. *NeuroImage*, 6(3), 218-229. doi: <http://dx.doi.org/10.1006/nimg.1997.0291>
- Frith, C. D., & Frith, U. (1999). Interacting minds--a biological basis. *Science*, 286(5445), 1692-1695.
- Frith, U., & Frith, C. (2010). The social brain: allowing humans to boldly go where no other species has been. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1537), 165-176. doi: 10.1098/rstb.2009.0160
- Fyock, J., & Stangor, C. (1994). The role of memory biases in stereotype maintenance. *British Journal of Social Psychology*, 33(3), 331-343. doi: 10.1111/j.2044-8309.1994.tb01029.x
- Gilbert, C. D., & Sigman, M. (2007). Brain States: Top-Down Influences in Sensory Processing. *Neuron*, 54(5), 677-696. doi: <https://doi.org/10.1016/j.neuron.2007.05.019>
- Gray, K. (2017). How to Map Theory: Reliable Methods Are Fruitless Without Rigorous Theory. *Perspect Psychol Sci*, 12(5), 731-741. doi: 10.1177/1745691617691949
- Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. *Proc Natl Acad Sci U S A*, 100(1), 253-258. doi: 10.1073/pnas.0135058100
- Greven, I. M., Downing, P. E., & Ramsey, R. (2016). Linking person perception and person knowledge in the human brain. *Social Cognitive and Affective Neuroscience*, 11(4), 641-651. doi: 10.1093/scan/nsv148
- Greven, I., Downing, P., & Ramsey, R. (2018, January 18). Neural networks supporting social evaluation of bodies based on body shape. Retrieved from psyarxiv.com/q4faj
- Greven, I. M., & Ramsey, R. (2017a). Person perception involves functional integration between the extrastriate body area and temporal pole. *Neuropsychologia*, 96, 52-60. doi: <http://dx.doi.org/10.1016/j.neuropsychologia.2017.01.003>
- Greven, I. M., & Ramsey, R. (2017b). Neural network integration during the perception of in-group and out-group members. *Neuropsychologia*, 106, 225-235.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn Sci*, 10(1), 14-23.

- Harel, A., Kravitz, D. J., & Baker, C. I. (2014). Task context impacts visual object processing differentially across the cortex. *Proceedings of the National Academy of Sciences*, 111(10), E962-E971. doi: 10.1073/pnas.1312567111
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223-233.
- Jack, R. E., & Schyns, P. G. (2017). Toward a Social Psychophysics of Face Communication. *Annu Rev Psychol*, 68, 269-297. doi: 10.1146/annurev-psych-010416-044242
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences*, 107(25), 11163-11170. doi: 10.1073/pnas.1005062107
- Kanwisher, N. (2017). The Quest for the FFA and Where It Led. *The Journal of Neuroscience*, 37(5), 1056-1061. doi: 10.1523/jneurosci.1706-16.2016
- Ma, N., Vandekerckhove, M., Van Overwalle, F., Seurinck, R., & Fias, W. (2011). Spontaneous and intentional trait inferences recruit a common mentalizing network to a different degree: spontaneous inferences activate only its core areas. *Social Neuroscience*, 6(2), 123-138.
- Macrae, C. N., & Quadflieg, S. (2010). Perceiving People *Handbook of Social Psychology*: John Wiley & Sons, Inc.
- McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. *NeuroImage*, 61(4), 1277-1286.
- Meehl, P. E. (1990). Appraising and Amending Theories: The Strategy of Lakatosian Defense and Two Principles that Warrant It. *Psychological Inquiry*, 1(2), 108-141. doi: 10.1207/s15327965pli0102_1
- Mitchell, J. P., Cloutier, J., Banaji, M. R., & Macrae, C. N. (2006). Medial prefrontal dissociations during processing of trait diagnostic and nondiagnostic person information. *Social Cognitive and Affective Neuroscience*, 1(1), 49-55. doi: 10.1093/scan/nsl007
- Molenberghs, P. (2013). The neuroscience of in-group bias. *Neuroscience & Biobehavioral Reviews*, 37(8), 1530-1536. doi: <http://dx.doi.org/10.1016/j.neubiorev.2013.06.002>
- Munafò, M. R., Nosek, B. A., Bishop, D. V. M., Button, K. S., Chambers, C. D., Percie du Sert, N., . . . Ioannidis, J. P. A. (2017). A manifesto for reproducible science. *Nature Human Behaviour*, 1, 0021. doi: 10.1038/s41562-016-0021
- O'Reilly, J. X., Woolrich, M. W., Behrens, T. E. J., Smith, S. M., & Johansen-Berg, H. (2012). Tools of the trade: psychophysiological interactions and functional connectivity. *Social Cognitive and Affective Neuroscience*, 7(5), 604-609. doi: 10.1093/scan/nss055
- Olson, I. R., McCoy, D., Klobusicky, E., & Ross, L. A. (2013). Social cognition and the anterior temporal lobes: a review and theoretical framework. *Social Cognitive and Affective Neuroscience*, 8(2), 123-133. doi: 10.1093/scan/nss119
- Over, H., & Cook, R. (2018). Where do spontaneous first impressions of faces come from? *Cognition*, 170, 190-200. doi: 10.1016/j.cognition.2017.10.002
- Park, H.-J., & Friston, K. (2013). Structural and Functional Brain Networks: From Connections to Cognition. *Science*, 342(6158).
- Peelen, M. V., & Downing, P. E. (2005). Selectivity for the Human Body in the Fusiform Gyrus. *J Neurophysiol*, 93(1), 603-608. doi: 10.1152/jn.00513.2004
- Pinsk, M. A., Arcaro, M., Weiner, K. S., Kalkus, J. F., Inati, S. J., Gross, C. G., & Kastner, S. (2009). Neural representations of faces and body parts in macaque and human cortex: a comparative fMRI study. *Journal of neurophysiology*, 101(5), 2581-2600.

- Pinsk, M. A., DeSimone, K., Moore, T., Gross, C. G., & Kastner, S. (2005). Representations of faces and body parts in macaque temporal cortex: a functional MRI study. *Proceedings of the National Academy of Sciences of the United States of America*, 102(19), 6996-7001.
- Pourtois, G., Peelen, M. V., Spinelli, L., Seeck, M., & Vuilleumier, P. (2007). Direct intracranial recording of body-selective responses in human extrastriate visual cortex. *Neuropsychologia*, 45(11), 2621-2625.
- Poyo Solanas, M., Zhan, M., Vaessen, M., Hortensius, R., Engelen, T., & de Gelder, B. (2018). Looking at the face and seeing the whole body. Neural basis of combined face and body expressions. *Social cognitive and affective neuroscience*, 13(1), 135-144.
- Puhl, R. M., & Heuer, C. A. (2009). The stigma of obesity: a review and update. *Obesity*, 17(5), 941-964.
- Quadflieg, S., Flannigan, N., Waiter, G. D., Rossion, B., Wig, G. S., Turk, D. J., & Macrae, C. N. (2011). Stereotype-based modulation of person perception. *NeuroImage*, 57(2), 549-557. doi: 10.1016/j.neuroimage.2011.05.004
- Ramsey, R., van Schie, H. T., & Cross, E. S. (2011). No two are the same: Body shape is part of identifying others. *Cognitive Neuroscience*, 2(3-4), 207-208. doi: 10.1080/17588928.2011.604721
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". *NeuroImage*, 19(4), 1835-1842.
- Sell, A., Cosmides, L., Tooby, J., Sznycer, D., von Rueden, C., & Gurven, M. (2009). Human adaptations for the visual assessment of strength and fighting ability from the body and face. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1656), 575-584.
- Sporns, O. (2013). Network attributes for segregation and integration in the human brain. *Curr Opin Neurobiol*, 23(2), 162-171. doi: 10.1016/j.conb.2012.11.015
- Sterzer, P., Kleinschmidt, A., & Rees, G. (2009). The neural bases of multistable perception. *Trends in Cognitive Sciences*, 13(7), 310-318. doi: <https://doi.org/10.1016/j.tics.2009.04.006>
- Suchan, B., Bauser, D. S., Busch, M., Schulte, D., Gronemeyer, D., Herpertz, S., & Vocks, S. (2013). Reduced connectivity between the left fusiform body area and the extrastriate body area in anorexia nervosa is associated with body image distortion. *Behav Brain Res*, 241, 80-85. doi: 10.1016/j.bbr.2012.12.002
- Tajfel, H., Billig, M. G., Bundy, R. P., & Flament, C. (1971). Social Categorization and Intergroup Behavior. *European Journal of Social Psychology*, 1(2), 149-177. doi: DOI 10.1002/ejsp.2420010202
- Taylor, J. C., Wiggett, A. J., & Downing, P. E. (2007). Functional MRI Analysis of Body and Body Part Representations in the Extrastriate and Fusiform Body Areas. *Journal of Neurophysiology*, 98(3), 1626-1633. doi: 10.1152/jn.00012.2007
- Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Hum. Brain Mapp.*, 30, 829.
- Wang, Y., Collins, J. A., Koski, J., Nugiel, T., Metoki, A., & Olson, I. R. (2017). Dynamic neural architecture for social knowledge retrieval. *Proceedings of the National Academy of Sciences*, 114(16), E3305-E3314.
- Zhan, M., Goebel, R., & de Gelder, B. (2018). Ventral and Dorsal Pathways Relate Differently to Visual Awareness of Body Postures under Continuous Flash Suppression. *eNeuro*, 5(1), ENEURO-0285.
- Zimmermann, M., Toni, I., & de Lange, F. P. (2013). Body posture modulates action perception. *Journal of Neuroscience*, 33(14), 5930-5938.

Figure 1. Functional segregation in body perception and social cognition.

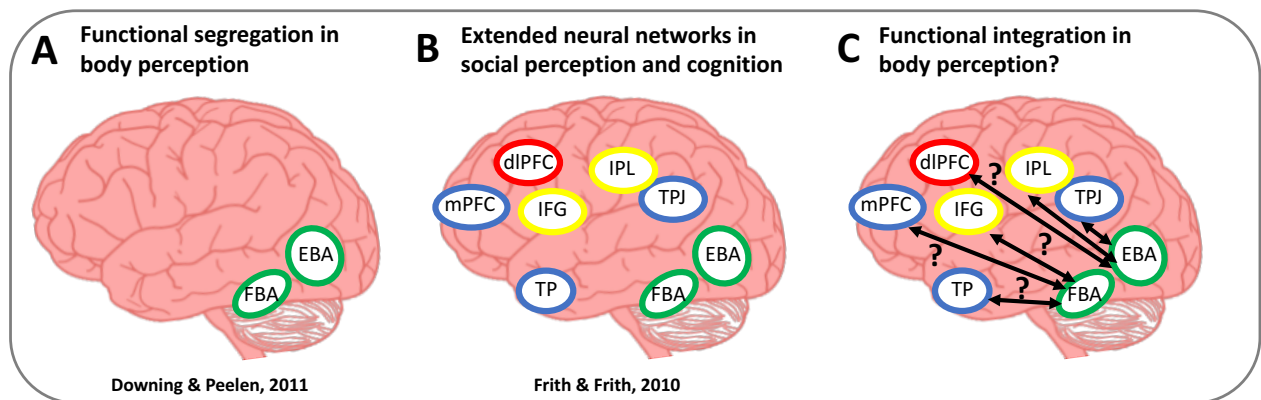


Figure 1. Functional segregation in body perception and social cognition. The majority of research investigating body perception (A) and social cognition (B) has focussed on understanding the role of functional segregation. Functional segregation is characterised by information processing that is carried out by functionally related brain regions that are arranged in modules. Less body perception research has investigated the role of functional integration between brain networks (C). Functional integration is characterised by the exchange of signals across a distributed set of brain networks or modules. Abbreviations: FBA = fusiform body area; EBA = extrastriate body area; mPFC = medial; prefrontal cortex; TP = temporal pole; TPJ = temporoparietal junction; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; dIPFC = dorsolateral prefrontal cortex. Colour scheme: Green = body-selective cortex; Blue = theory-of-mind network; Yellow = mirror neuron system; Red = executive control circuit.

Figure 2. Functional integration in body perception.

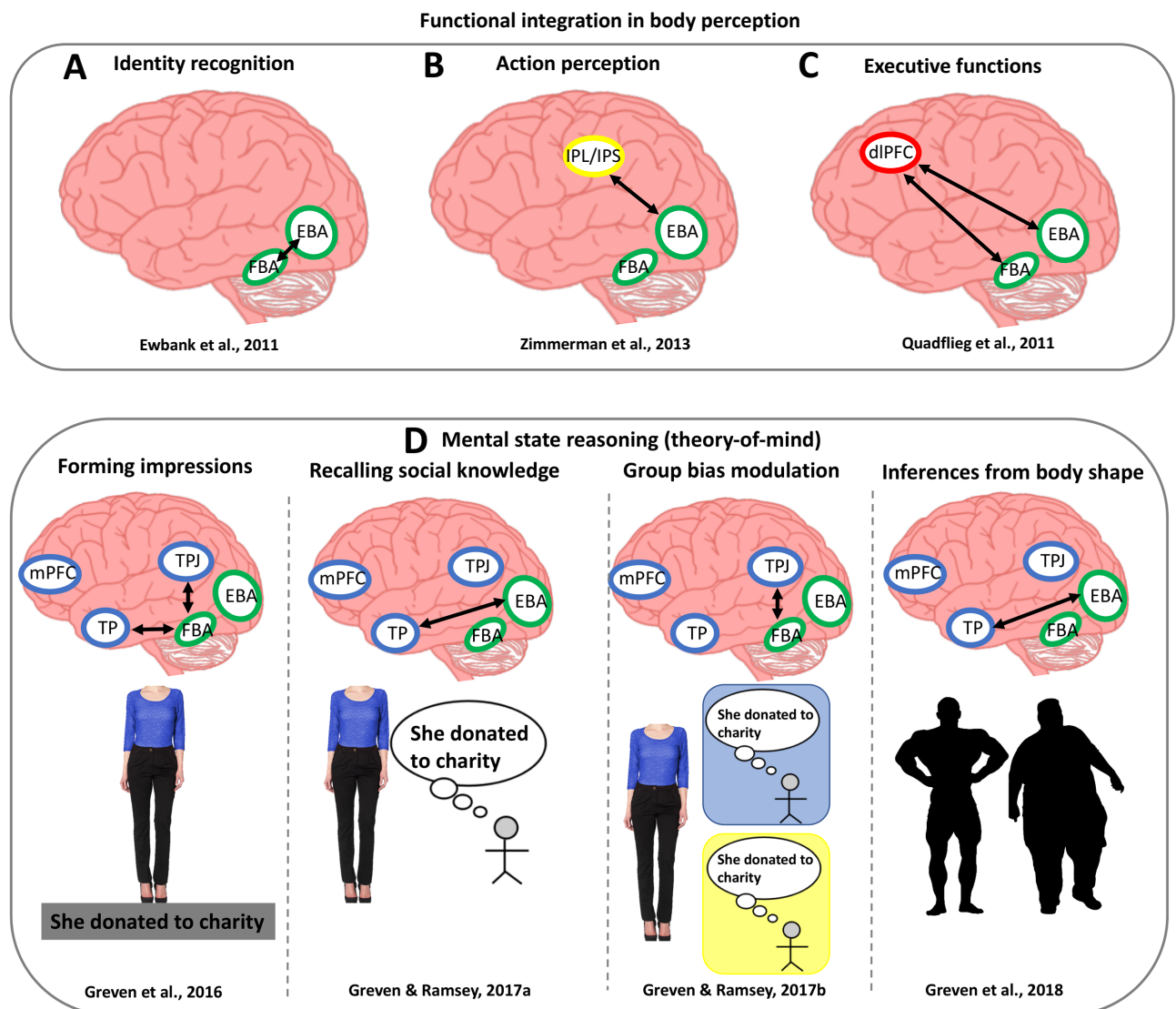


Figure 2. Functional integration in body perception. A summary of fMRI studies that have investigated functional integration in body perception. These studies have used measures of functional connectivity to estimate links within the ventral visual stream during identity processing (A) as well as between the ventral visual stream and networks associated with action perception (B), executive functions (C) and theory-of-mind (D). Abbreviations and colour scheme as Figure 1.